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THE INFLUENCE OF SIZE OF QUADRAT
ON THE DISTRIBUTIONAL PATTERNS
OF PLANT POPULATIONS

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INTRODUCTION

THE quadrat, a two-dimensional unit of fixed size and shape, generally square but sometimes circular or rectangular, has been one of the principal sampling devices used by ecologists for the past fifty years. From the time of Raunkiaer and Clements, it has been widely employed in gathering quantitative, semiquantitative, or pseudoquantitative information about the structure and organization of plant communities and about the distributional patterns of individual species. The quadrat technique has great practical advantages in field work, for it often requires nothing more than a record of presence or absence, or at most a count of the individuals present. From time to time, however, it has been subjected to considerable criticism. Gleason (1920) seems to have been one of the first to appreciate the fact that the number of individuals likely to be found in a quadrat depended in part upon the size of quadrat employed, and he realized that any statistics resulting from quadrat sampling were influenced accordingly. Since 1920 the shortcomings and imperfections

of the quadrat method have become increasingly apparent, and in recent years the ways in which size and number of quadrats affect ecological data have been explored much more precisely. Much of the literature on this subject has been recently reviewed by Curtis and McIntosh (1950). Important additional papers include those of Archibald (1949a, 1949b) and Williams (1950).

A good deal of our knowledge about the effects of quadrat size has been derived from artificially constructed populations (McGinnies, 1934; Penfound, 1945; Curtis and McIntosh, 1950). Opportunity to apply this knowledge to natural populations was provided by a study of three species (*Lespedeza capitata*, *Liatris aspera*, and *Solidago rigida*), components of an old-field grassland community on the Edwin S. George Reserve, of the University of Michigan, Livingston County, southeastern Michigan. A preliminary description of this community has recently been published (Evans and Cain, 1952), and the positions of individual plants of these three species as they occurred on an area of approximately two acres within the community have been mapped and charted (Cain and Evans, 1952). For each of these populations, the frequency data obtained by using a quadrat size of one square meter have been subjected to analysis from the standpoint of "contagious" distribution functions by Thomson (1952). In the present paper these populations have been re-examined by employing quadrats of several sizes, and a comparison of the results is provided as a demonstration of the influence of quadrat size on distributional data.

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METHODS

The map prepared by Cain and Evans (1952) was subdivided into quadrats, each of which was four meters square. This yielded a total of 429 quadrats lying completely within the boundaries of the mapped populations and covering an area of 6864 square meters. These quadrats were then further subdivided into a series of increasingly smaller units, each subdivision doubling the number of quadrats and halving their size. The full series consisted of the following quadrat sizes: 16, 8, 4, 2, 1, 1/2, 1/4, 1/8, and 1/16 square meters, respectively.

The number of individual plants occurring in each quadrat of each size was recorded for all three species under study. All quadrats of each size were examined, so that the total area and the total population remained constant for the entire series. Differences in the results for the different quadrat sizes are, therefore, not due to errors of random sampling.

MATERIAL

Within the 6864 square meters covered by this study, there were 696 *Lespedeza*, 388 *Solidago*, and 298 *Liatris* plants, respectively. Calculated values of density (number of plants per square meter) are as follows: *Lespedeza*, 0.1014; *Solidago*, 0.0565; and *Liatris*, 0.0434. Thus, these populations displayed a low order of density — very much lower, for example, than that exhibited by the two dominant grasses of the community, *Poa compressa* and *Aristida purpurascens*, each of which exceeded 500 culms per square meter (Evans and Cain, 1952). These density values do not represent minimal ones in this community, however, for they are considerably higher than those shown by such species as *Lactuca pulchella*, *Tragopogon pratensis*, and *Lithospermum croceum*. They are, in fact, quite typical of the sort of values the field ecologist frequently encounters.

On the basis of frequency (per cent of the total number of quadrats which represent occupied ones) data obtained from meter-square quadrats, Thomson (1952) has pointed out that the distributions of all of these populations depart radically from expectation for randomly distributed values. The comparison of data from such strongly skewed populations presents considerable difficulty, but it must again be emphasized that biologists are commonly faced with material of this sort.

RESULTS

Relation of Density to Quadrat Size

When expressed as the number of individuals per unit of area, density values obviously remain constant regardless of quadrat size. If density is defined as the number of individuals per quadrat, however, it is clear that density becomes directly proportional to quadrat size, doubling in value with each two-fold increase of quadrat area (Table I). In either case, two or more species will maintain similar density relationships for every quadrat size. As indicated above, the three species here examined may be listed in order of decreasing density as follows: *Lespedeza*, *Solidago*, and *Liatris*.

Relation of Frequency to Quadrat Size

The same relationships do not hold for frequency values for these species (Table I). In no case is there a constant doubling of frequency with doubling of quadrat size; in fact, the rate of increase in frequency lessens with each increase in size of quadrat. The frequency relationships among the three species also change as the quadrat size changes. *Solidago*, for example, which is only slightly more frequent than *Liatris* and roughly half as frequent as *Lespedeza* in the smallest quadrats, is twice as frequent as *Liatris* and one-and-one-half times as frequent as *Lespedeza* in the largest quadrats. Estimates of relative frequency, then, are affected by the size of quadrat employed.

TABLE I.

Relation Of Density (Number of Plants Per Quadrat Examined), Frequency (Per Cent of Quadrats Occupied), and Abundance (Number of Plants Per Occupied Quadrat) to Quadrat Size for Three Component Species of an Old-Field Community, Edwin S. George Reserve, Livingston County, Michigan

Quadrat Size (sq. m.)	Number of Quadrats	Number of occupied quadrats			Density			Frequency			Abundance		
		Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago
0.0625	109,824	658	292	386	0.0063	0.0027	0.0035	0.60	0.27	0.35	1.06	1.02	1.01
0.125	54,912	626	285	382	0.0127	0.0054	0.0071	1.14	0.52	0.70	1.11	1.05	1.02
0.25	27,456	566	274	378	0.0254	0.0109	0.0141	2.06	1.00	1.38	1.23	1.09	1.03
0.5	13,728	497	253	366	0.0507	0.0217	0.0283	3.62	1.84	2.67	1.40	1.18	1.07
1.	6,864	401	221	340	0.1014	0.0434	0.0565	5.84	3.22	4.95	1.74	1.35	1.14
2.	3,432	308	185	318	0.2028	0.0868	0.1131	8.97	5.39	9.27	2.26	1.61	1.22
4.	1,716	224	152	291	0.4056	0.1737	0.2261	13.05	8.86	16.96	3.12	1.96	1.33
8.	858	170	124	243	0.8111	0.3473	0.4522	19.81	14.45	28.32	4.09	2.40	1.60
16.	429	120	92	184	1.6224	0.6947	0.9044	27.97	21.45	42.89	5.80	3.24	2.11

Relation of Abundance to Quadrat Size

Abundance is here defined as the number of individuals per occupied quadrat. Values of abundance for *Lespedeza*, *Liatris*, and *Solidago* are also shown in Table I. Although these species retain the same order of relative abundance throughout the series of quadrat sizes, the differences among the abundance values become greater with increased quadrat size, but not proportionally so. This is clearly to be expected when the species being compared have distribution patterns showing different degrees of clumping. Curtis and McIntosh (1950) point out that abundance is derived from both density and frequency, having the following relationship to them: $\text{abundance} = 100 \times \text{density/frequency}$, where frequency is a percentage and density is the number of individuals per quadrat. It should be noted that for the smallest quadrat size (0.0625 square meters) the three species are almost equally abundant, each approaching the minimal value of 1.00. Thus the size of quadrat employed may determine one's estimate of relative abundance.

Relation of Frequency Distribution to Quadrat Size

Table II indicates the changes in frequency distribution which appear when the size of quadrat is altered. The most obvious result of increasing quadrat size is a lengthening of the tail of the distribution. The larger the quadrat, the more likely it is to contain many individuals and the less likely it is to have none. As more and more of the individuals present are found together in the larger quadrats, the number of quadrats containing only one individual decreases with each larger quadrat size, but, due to the reduction in total number of quadrats, the absolute frequency with which this class occurs actually increases. Quadrats with two or three individuals show a gradual increase in numbers up to a certain quadrat size, beyond which they decline. Some indication of the differences in degree of clumping shown by these species is seen in the data for the largest quadrats; as many as 63 *Lespedeza* plants were recorded in a single 16-square-meter quadrat, where the number of *Solidago* present never exceeded 14.

The data for each quadrat size have been fitted to a Poisson series, using the chi-square test for comparison with the values expected for randomly distributed populations. The chi-squares for *Lespedeza* and *Liatris* indicate highly significant departures from expectation for all quadrat sizes. This is true also for *Solidago* with the exception of the chi-square for the smallest quadrat size, which does not show any significant difference between the observed and the expected distribution. In this latter case, the size of the quadrat has been so reduced that the occurrence of more than one individual per quadrat is an extremely rare event. Preston (1948) has made the point that, for the Poisson distribution laws to apply, there must be room in the quadrat for more individuals than actually occur. The data in Table II suggest that a quadrat 1/16 of a square meter in area approaches the lower limits of space required by individual plants of these three species under present conditions within the community.

TABLE II

Relation of Frequency Distribution to Quadrat Size for Three Component Species of an Old-field Community, Edwin S. George Reserve, Livingston County, Michigan

Plants Per Quadrat	Quadrat Size in Square Meters								
	0.0625	0.1250	0.2500	0.5000	1.0000	2.0000	4.0000	8.0000	16.0000
Lespedeza									
0	109,166	54,286	26,890	13,231	6,463	3,124	1,492	688	309
1	622	566	465	362	250	164	98	68	44
2	34	50	83	98	80	58	42	24	15
3	2	10	11	24	37	30	29	21	12
4	0	0	4	5	14	19	13	11	6
5			2	3	11	11	6	6	6
6			1	4	3	12	7	8	4
7			0	1	4	5	6	8	2
8				0	1	2	4	0	3
9					0	4	5	4	1
10					1	2	3	3	4
11					0		3	5	2
12						0	3	3	2
13						0	0	2	2
14						0	1	2	2
15						0	2	1	2
16						1	0	1	5
17						0	0	0	2
18							0	0	1
19							1	0	2
20							0	0	0
21							0	0	1
22							1	0	0
23							0	0	0
29								1	0
34								2	0
37								0	1
63									1
64 or more									0
Chi- square	498.4	704.2	938.0	955.4	661.2	460.7	769.6	813.8	918.6

TABLE II (Cont.)

Plants Per Quadrat	Quadrat Size in Square Meters								
	0.0625	0.1250	0.2500	0.5000	1.0000	2.0000	4.0000	8.0000	16.0000
Liatris									
0	109,532	54,627	27,182	13,475	6,643	3,247	1,564	734	337
1	286	272	252	218	169	125	92	68	40
2	6	13	20	28	37	34	28	20	19
3	0	0	2	5	9	16	19	16	6
4			0	1	3	3	4	9	7
5				1	2	3	3	4	3
6				0	1	1	1	1	4
7					0	1	1	1	1
8						1	0	0	3
9						1	0	2	0
10						0	2	0	1
11							1	0	0
12							1	0	0
21							0	1	1
22								1	0
43								0	1
44 or more									0
Chi- square	15.5	173.4	139.1	340.7	379.7	270.7	169.6	342.9	194.8
Solidago									
0	109,438	54,530	27,078	13,362	6,524	3,114	1,425	615	245
1	384	376	368	344	295	258	222	162	94
2	2	6	10	22	42	52	51	48	36
3	0	0	0	0	3	6	13	20	31
4					0	2	2	5	8
5						0	2	4	10
6							0	1	0
7							1	1	2
8							0	1	0
9								1	1
10								0	1
14									1
15 or more									0
Chi- square	3.66	15.3	20.4	55.1	126.9	100.9	52.9	97.9	107.9

The Poisson series evidently does not provide a basis for an adequate representation of these contagiously distributed species. Thomson (1952) found it necessary to use a more complex distribution function for the treatment of the data obtained from the one-square-meter quadrats. Similar considerations evidently obtain for the other quadrat sizes.

Relation of Measure of Dispersion to Quadrat Size

One of the most important features of any distributional pattern is the degree to which it departs from random expectation. To measure this dispersion, a number of ecologists, including Blackman (1942), have made use of the well-known fact that in the Poisson series the variance is equal to the mean. This measure assumes that the extent to which the variance:mean ratio deviates from unity will express the departure from randomness, and, vice versa, that the more nearly it approaches a value of 1.00 the greater the conformity to a random distribution. Other workers have tried to exploit the relationship that exists between frequency and density in a randomly distributed population. This relationship can be expressed by the formula

$$F = 100 (1 - e^{-D})$$

where F is frequency, D is density and e is the base of the natural or Napierian logarithms (Curtis and McIntosh, 1950). For random distributions, then, it is possible to calculate density values for any known level of frequency. McGinnies (1934) used this fact to obtain the ratio between the observed density and the density calculated from frequency values. Here also departure from unity is taken to indicate degree of nonrandomness. Fracker and Brischle (1944) modified this measure by taking the ratio of the difference between observed and expected densities to the square of the expected density. Whitford (1949) employed the ratio of abundance to frequency, or, since abundance is equal to the density divided by the frequency index, the ratio of the density to the square of the frequency. The effects of quadrat size upon each of these four measures of dispersion have been considered by Curtis and McIntosh (1950) with examples drawn from artificially constructed random, regular, and contagious population distributions. When their populations were clumped, all of these measures proved to be dependent upon quadrat size, and Whitford's measure was shown to be so sensitive that its use is not recommended for species whose density is such as to give frequencies of less than 20 per cent.

Table III gives the values of these four measures of dispersion for the *Lespedeza*, *Liatris*, and *Solidago* populations as calculated for each size of quadrat. For Blackman's and McGinnies' measures, in which a value greater than unity is said to indicate a tendency to clumping, the effect of quadrat size is readily observed; the difference between successive values is not directly proportional to size of quadrat but becomes greater with each increase of quadrat size. It should be noted that the values of both of these measures for the smallest-sized quadrats used in this study, approach the theoretical value of 1, expected for a random

TABLE III
Effects of Quadrat Size on Various Measures of Dispersion for Three Component Species in an Old-field Community, Edwin S. George Reserve, Livingston County, Michigan
 V = variance, $\bar{x}$ = mean density, D = actual density, d = expected density, F = frequency.

Quadrat Size (sq.m.)	Blackman (1942)			McGinnies (1934)			Whitford (1949)			Fracker and Brischle (1944)		
	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago
0.0625	1.102	1.038	1.007	1.0289	1.0192	1.0028	1.7657	3.8373	2.8595	4.6916	7.1983	0.8025
0.125	1.217	1.082	1.024	1.1055	1.0429	1.0122	0.9753	2.0205	1.4599	9.2085	8.2349	1.7439
0.25	1.478	1.164	1.038	1.2171	1.0822	1.0195	0.5965	1.0900	0.7700	10.4207	8.1909	1.4063
0.5	1.843	1.341	1.085	1.3749	1.1669	1.0441	0.3868	0.6391	0.3976	10.1655	8.9697	1.6278
1.	2.586	1.742	1.206	1.0845	1.3266	1.1127	0.2971	0.4188	0.2304	11.3707	9.9792	2.2181
2.	3.864	2.424	1.310	2.1568	1.5670	1.1627	0.2518	0.2988	0.1317	12.3024	10.2013	1.6735
4.	6.319	3.399	1.512	2.8996	1.8724	1.2168	0.2380	0.2213	0.0786	13.5805	9.4062	1.1666
8.	9.809	5.874	1.983	3.6736	2.2251	1.3581	0.2066	0.1663	0.0564	14.1589	7.8483	1.0754
16.	15.319	12.193	2.633	4.9445	2.8779	1.6145	0.2074	0.1510	0.0492	12.0218	7.7799	1.4156

distribution, whereas it has already been demonstrated that these populations are not randomly distributed. Furthermore, the values for the three species are very nearly alike at this lower level, apparently indicating little difference among them. If, then, the data for the smallest quadrats had been the only material available, these measures would give a false impression of the situation.

The values for Whitford's index also show a clear-cut relationship to quadrat size, and their range is indicative of the sensitivity of the measure to this factor. In other respects, Whitford's measure differs from those of Blackman and McGinnies, for it shows its greatest percentage differences between successive values at the smallest quadrat sizes. Since, in this measure, the lower the value the closer the approximation to a random distribution, these data seem to suggest that the smallest-sized quadrats indicate a greater departure from randomness than do the quadrats of larger size, which is just the reverse of the picture obtained from the measures of McGinnies and Blackman. If the three species are compared on the basis of Whitford's measure, their relative positions are found to shift as the quadrat size is altered; this is expected because this measure makes use of frequency values, and differences in relative frequency have already been indicated (Table I.). For the four smaller quadrat sizes ($1/16$, $1/8$, $1/4$, and $1/2$ square meters) Lespedeza is rated most random, Solidago next, and Liatris least; for the 1- and 2-square-meter quadrats, Solidago is most random, Lespedeza next, and Liatris least; and for the three larger quadrats (4, 8, and 16 square meters), Solidago is most random, Liatris next, and Lespedeza least.

Fracker and Brischle's measure proved unique in not exhibiting any definite relationship to size of quadrat, although the values were clearly affected by it. This measure, like that of Whitford, approaches zero for random distributions. It gives the greatest degree of differentiation among the three species at any given quadrat size. Its values agree with those of Blackman's and McGinnies' measures in assigning the most nearly random distribution to Solidago, but the three species do not maintain similar relationships throughout the series, for Lespedeza shifts from an intermediate position for the smallest quadrat size to the least randomly distributed for all larger-sized quadrats.

All of these measures are clearly influenced by the size of the quadrat used to obtain the basic data. It seems likely that disagreement in the results of various authors stems in part from differences in the sizes of their quadrats, and that success or failure in the application of these measures depends upon a fortunate or unfortunate choice of quadrat size.

DISCUSSION

As noted above, the smallest-sized quadrats yielded values for Blackman's measure involving the ratio of the variance to the mean which closely approximate unity, as expected for randomly distributed populations. A hypothetical example will be given to show that a distribution may depart radically from that of a Poisson series and still have a variance exactly equal to the mean. If 101 individuals are distributed

in 101 quadrats in such a way that 37 quadrats contain 0 individuals, 38 contain 1, 18 contain 2, 6 contain 3, 1 contains 4, and 1 contains 5, both the mean density and the variance will be found to equal 1.00, and a chi-square test gives a value of 0.036 (d.f. = 1), which does not indicate any significant difference from a Poisson distribution. However, if these same 101 individuals are distributed among the same 101 quadrats in such a way that 20 quadrats contain 0 individuals; 76 contain 1; and 5 contain 5, the variance is still equal to the mean density, that is, 1.00, but a chi-square test gives a value of 75.17 (d.f. = 1), indicating a highly significant departure from a Poisson distribution. Thus, as Thomson (1952) has pointed out, disagreement of observed values with those expected for the Poisson distribution certainly indicates some kind of nonrandom arrangement, but agreement by no means necessarily implies that the observed distribution is a random one. Measures which employ the ratio of the variance to the mean as a coefficient of dispersion are therefore not completely reliable.

Measures of dispersion which are based on the relation between density and frequency in a randomly distributed population are also open to objections. This relation does not fully describe the population distribution; it considers only the over-all mean density and the zero class of the frequency distribution. An adequate distribution description should take into account the form or shape of the distribution curve, and the contributions to the departure from randomness that may be made by classes other than the zero class. In contagiously distributed populations some one class may contribute a major part of the total dispersion. For example, in the frequency distribution for the *Liatris* data obtained from the smallest-sized quadrats (Table II), the class containing two individuals per quadrat contributed almost all of the departure from randomness (15.1 out of the total chi-square of 15.5). I have already indicated the effect that quadrat size may have upon the frequencies with which contagiously distributed populations occur in quadrats. Any evaluation of dispersion which is based on frequency will therefore be influenced by the size of quadrat used in obtaining the frequency values.

Similar criticism appears to be equally applicable to measures based in part upon the density calculated from frequency values, for this calculated density is really that which is expected for a random distribution. If the frequency is very low, of the order of 0.10 or less, the frequency-density relationship expressed by the formula given above is closely approximated for contagious distributions, provided that the quadrat size is such as to make the occurrence of more than one individual per quadrat a rare event. Where greater frequencies occur, however, or if quadrats including several to many individuals are often encountered, contagiously distributed populations do not exhibit the expected relationship between density and frequency, and it becomes impossible to calculate one from the other.

In sampling plant populations in the field, ecologists have ordinarily employed only one quadrat size in any given investigation. The above demonstration of the different results obtained with large and small quadrats, however, indicates a source of considerable error in the one-quadrat approach and suggests the desirability of utilizing several sizes

of quadrat in securing samples for the study of distribution patterns and other phytosociological characters. The extra time and labor involved is not excessive, and the additional information obtained is well worth the cost. With material obtained by quadrats of several sizes, it is possible to put the frequency-density relationship to practical use. With randomly distributed populations, if frequency is plotted against density for each quadrat size, the points will be found to lie on a characteristic curve (Fig. 1). Corresponding data for any nonrandom population may be plotted in similar fashion, and the resulting curve can be compared with the one for the theoretical random distribution. This has been done in Figure 1 for the observed populations of *Lespedeza*, *Liatris*, and

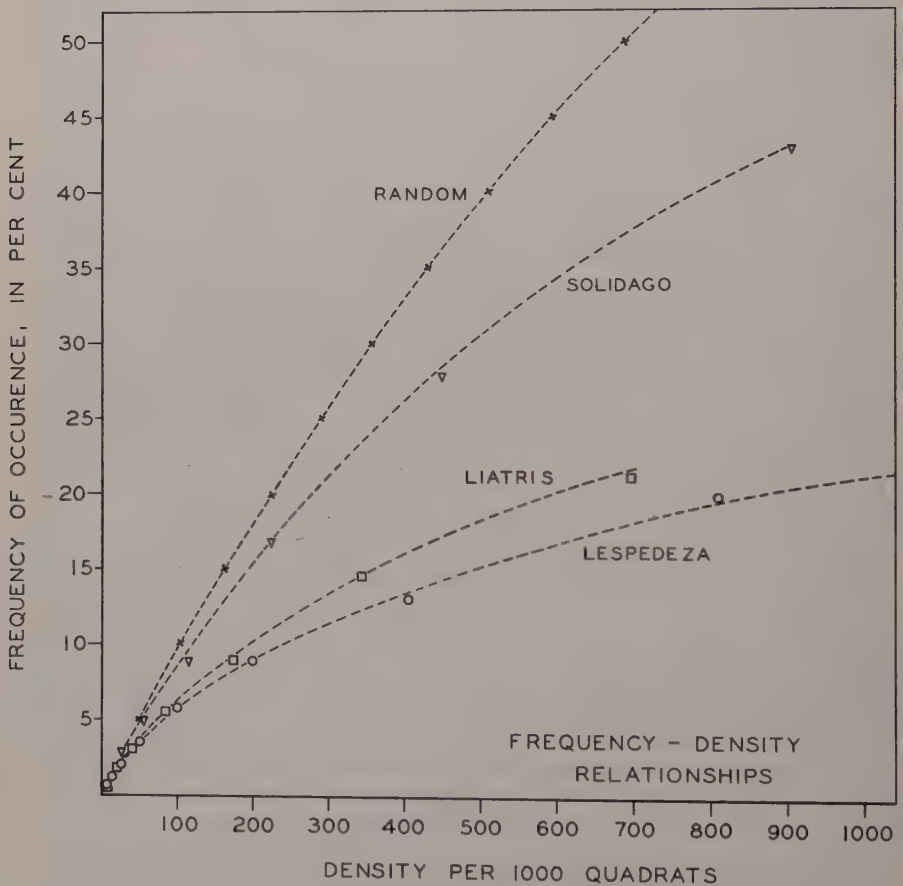


FIG. 1. Frequency-density relationships for a random distribution and for populations of three component species of an old-field community, Edwin S. George Reserve, Livingston County, Michigan.

Solidago. The tendency to contagious distribution is shown by a flattening of the theoretical curve, while departure from randomness in the opposite direction, that is, towards greater regularity of occurrence, would be indicated by a curve steeper than that for the random distribution. Each of the observed populations evidently departs markedly from randomness, with Solidago displaying the greatest degree of conformity to a random distribution, and Lespedeza the least. This is in harmony with the estimation of relative clumping observable in the field or by inspection of the mapped distribution patterns, but the divergence of the curves gives a clearer picture of the degree to which these populations depart from randomness. Similar curves were derived by Curtis and McIntosh (1950) in sampling artificial populations, and there is good agreement here between their theoretical data and those obtained from field studies.

In conclusion then, values of many phytosociological characteristics which are estimated from a single quadrat size may give an erroneous impression, especially if the species concerned are strongly clumped. If quadrats of several sizes are employed in collecting data, the frequency-density curve that can be derived will enable one to determine, qualitatively at least, the degree to which the observed distributions depart from randomness and by extrapolation or interpolation to compare two or more sets of data obtained with quadrats of different size.

SUMMARY

The distributional patterns of populations of *Lespedeza capitata*, *Liatris aspera*, and *Solidago rigida* occurring in an old-field grassland community in southeastern Michigan have been subjected to analysis by quadrats of several different sizes. The size of quadrat was found to affect the resulting values of frequency and abundance, as well as the frequency distributions of the number of individuals per quadrat. It was also shown to have a marked effect upon various measures of dispersion. This demonstration suggests the desirability of utilizing several sizes of quadrat in securing samples for the study of distribution patterns and other phytosociological characteristics. If data for several quadrat sizes are available, a frequency-density curve may be derived that will enable one to determine qualitatively the degree to which the observed distributions depart from randomness and to compare material obtained with quadrats of different size.

LITERATURE CITED

ARCHIBALD, E. A. A.

- 1949a The specific character of plant communities. I. Herbaceous communities. *Journ. Ecol.*, 37: 260-73.
1949b The specific character of plant communities. II. A quantitative approach. *Journ. Ecol.*, 37: 274-88.

BLACKMAN, G. E.

- 1942 Statistical and ecological studies on the distribution of species in plant communities. *Ann. Bot.*, 6: 351-66.

CAIN, S. A., and F. C. EVANS

- 1952 The distribution patterns of three plant species in an old-field community in southeastern Michigan. *Contrib. Lab. Vert. Biol. Univ. Mich.*, 52.

CURTIS, J. T., and R. P. McINTOSH

- 1950 The interrelations of certain analytic and synthetic phytosociological characters. *Ecology*, 31: 434-55.

EVANS, F. C., and S. A. CAIN

- 1952 Preliminary studies of the vegetation of an old-field community in southeastern Michigan. *Contrib. Lab. Vert. Biol. Univ. Mich.*, 51.

FRACKER, S. B., and H. A. BRISCHLE

- 1944 Measuring the local distribution of *Ribes*. *Ecology*, 25: 283-303.

GLEASON, H. A.

- 1920 Some applications of the quadrat method. *Bull. Torrey Bot. Club*, 47: 21-33.

McGINNIES, W. G.

- 1934 The relation between frequency index and abundance as applied to plant populations in a semi-arid region. *Ecology*, 15: 263-82.

PENFOUND, W. T.

- 1945 A study of phytosociological relationships by means of aggregations of colored cards. *Ecology*, 26: 38-57.

PRESTON, F. W.

- 1948 The commonness, and rarity, of species. *Ecology*, 29: 254-83.

THOMSON, G. W.

- 1952 Measures of plant aggregation based on contagious distributions. *Contrib. Lab. Vert. Biol. Univ. Mich.*, 53.

WHITFORD, P. B.

- 1949 Distribution of woodland plants in relation to succession and clonal growth. *Ecology*, 30: 199-208.

WILLIAMS, C. B.

- 1950 The application of the logarithmic series to the frequency of occurrence of plant species in quadrats. *Journ. Ecol.*, 38: 107-38.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price \$0.25.

